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A Life-Span Perspective on Interaction Between the Cerebral Hemispheres

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This issue of *Developmental Neuropsychology* is designed to examine recent advances in our understanding of how interaction between the cerebral hemispheres can change with age. An enhanced appreciation of the degree to which lateralization of function influences mental processing was spurred by research in the 1970s and beyond (e.g., Davidson & Hugdahl, 1995). The knowledge that the left hemisphere is best suited for processing information in a piecemeal, analytic manner, whereas the right hemisphere is best suited for processing information in a holistic or gestalt manner has filtered down to popular culture, as reflected in everything from advertisements to songs. Such representations often depict the hemispheres as unlikely bedfellows—the verbal left hemisphere and the spatial right hemisphere, or the analytic left hemisphere and the intuitive right hemisphere. Research with split-brain patients was startling, because in the absence of a corpus callosum, which normally functions to integrate the activity of the hemispheres, each hemisphere's abilities appeared in stark relief. By disconnecting them, it became clear exactly what an “odd couple” the hemispheres are.

Given that lateralization of function is a hallmark of human brain organization, it seems increasingly important to investigate how such seemingly ill-suited part-

ners ever manage to integrate their processing to produce the seamless behavior that we all experience. Of course, this question of the consequences of functional connectivity between brain regions is not limited to questions of how the hemispheres interact (e.g., Paus et al., 1997). However, using interaction between the hemispheres to address this fundamental question of brain organization is particularly attractive for a number of reasons. First, investigating hemispheric integration is experimentally very tractable in a noninvasive manner. Furthermore, knowledge gained from studies of intact individuals can be examined against the backdrop of the large body of research that has examined individuals who have had the cerebral commissures surgically severed (split-brain patients); individuals in whom the corpus callosum has failed to develop (i.e., those with agenesis of the corpus callosum [ACC]); and those with suspected damage to callosal fibers caused by disease or trauma (phenylketonuria, multiple sclerosis, traumatic brain injury).

The articles in this issue investigate some of the important questions regarding integration of information between the hemispheres from a life-span perspective, ranging from childhood through the older adult years. These articles include information from individuals of differing age with intact commissures, those with congenital absence of the corpus callosum, and those with presumed disease-related callosal damage—allowing for the strength of converging perspectives.

THE CORPUS CALLOSUM AND CHILD DEVELOPMENT

From a developmental perspective, one of the most important structural changes in the brain that is likely to affect interhemispheric interaction is the increasing myelination of the corpus callosum. Although the classic work on callosal development (Yakovlev & Lecours, 1967), which was based on postmortem samples, suggested that this process was completed by late childhood, the advent of magnetic resonance imaging has revealed that myelination continues much later than was initially thought. Increases in callosal myelination occur well into the late teenage years, suggesting that the corpus callosum is one of the latest structures to myelinate (Giedd et al., 1996). Hence, a primary question of interest is whether these changes in myelination have behavioral consequences. This question is addressed in a variety of ways in different articles within this issue.

Hagelthorn, Brown, Amano, and Asarnow (this issue) examined two measures of interhemispheric processing—one physiological and the other behavioral—and determined their relation. Because advancing age during childhood is associated with increased myelination and decreased interhemispheric transfer time, it has been assumed that decreased transfer time would have behavioral consequences. Hagelthorn et al. put this idea to the test. They obtained estimates of interhemispheric transfer time from visual event-related potentials (ERPs) acquired during perfor-

mance of a matching task. This task examined the degree to which match decisions were facilitated when two items to be compared were divided across the hemispheres rather than being directed to the same hemisphere (i.e., the degree of the bilateral field advantage). These researchers found clear evidence of a reduced bilateral field advantage with age and a trend indicating a reduction in interhemispheric transfer time based on the N1 (first negative wave) component of the ERP. However, the two measures were not significantly correlated, indicating that they may measure different aspects of callosal function. Nevertheless, these data provide evidence that age-related increases in myelination have a behavioral consequence in more rapid interhemispheric transfer and more accurate and efficient comparison of the information between the hemispheres.

Corroborating this viewpoint is another article within this issue. Chicoine, Proteau, and Lassonde (this issue) found that the incomplete callosal myelination in young children can have rather severe behavioral consequences. They demonstrate that the corpus callosum of young children aged 6 to 7 years cannot support the transfer of a learned visuomotor skill from one hand (and hence one hemisphere) to the other. In a particularly elegant demonstration, these authors show the striking similarity between the performances of young children and those of individuals with ACC who lack a corpus callosum, revealing how inadequate the immature callosum is for transferring certain types of information.

In contrast, the article by Banich, Passarotti, and Janes (this issue) suggests a developmental trend in bilateral visual matching that is somewhat different than that reported by Hagelthorn et al. (this issue) and that appears to be the consequence of intrahemispheric limitations in processing resources. In adults, interaction between the hemispheres is more beneficial to performance when tasks are computationally complex as compared to simple (e.g., Banich & Belger, 1990; Belger & Banich, 1992). This division of processing, allowed by a hemispheric splitting and then callosal reintegration of information, also appears to be especially helpful whenever the computational resources of particular individuals are taxed. For the most complex version of the Banich, Passarotti, and Janes task, younger school-age children showed evidence of benefitting more from a division of processing than did older children; that is, they showed a larger bilateral advantage.

It is instructive to consider both the convergence and divergence among these studies. Even though they use children of different age ranges and different methods, there is a convergence in that these studies all suggest that interhemispheric interaction changes during childhood. The studies diverge in that they suggest different developmental changes for different tasks or measures of interhemispheric interaction and callosal function. In many ways, divergent findings are not surprising. First, there are differences across the studies in task and stimulus complexity, as already mentioned. Although both Hagelthorn et al. (this issue) and Banich, Passarotti, and Janes (this issue) used bilateral and unilateral letter-matching tasks, the complexities of the tasks were very different, and the consequent outcomes

with respect to child development differed. The bilateral advantage that was larger in older children who performed the very simple matching task of Hagelthorn et al. became a bilateral advantage that was larger with younger children who performed the much more computationally complex task of Banich, Passarotti, and Janes. Apparently the simpler task could be done well by a single hemisphere. Thus, an increasing bilateral advantage with age reflected the ease of callosal transfer. However, the Banich, Passarotti, and Janes task exhausted the information-processing resources of the single hemisphere of the younger child; thus, an additional variable came into play—that of the computational gain provided by dividing processing across the hemispheres. In the study of Chicoine et al. (this issue), bihemispheric stimulus comparisons were not at issue. Nevertheless, the complex motor skill that was learned by the dominant hand (hemisphere) did not transfer to the other hemisphere in the younger children, whereas transfer was clearly present for older children. Here the critical variable is the insufficient channel capacity of the corpus callosum to mediate transfer of a complex learned motor skill.

In addition, divergent findings may relate to the fact that different tasks place demands on different callosal channels. The corpus callosum consists of over 250 million nerve fibers, and different sections of the callosum are likely to be tapped by the different paradigms used in these studies. For example, the measures of interhemispheric transfer time derived from the visual ERP likely reflect functioning of the splenium of the corpus callosum, which interconnects regions of extrastriate cortex, which is the where the visual N1 is generated (Brown, Jeeves, Dietrich, & Burnison, 1999; Clark & Hillyard, 1996; Simpson, Foxe, Vaughan, Mehta, & Schroeder, 1995). In contrast, the visuomotor learning task used by Chicoine et al. (this issue) is more likely to reflect functioning of parietal or central cortices, and hence of regions of the callosum more anterior to the splenium. It is not clear exactly what portion of the callosum is required by the Banich and Belger task used by Banich, Passarotti, and Janes (this issue) or by the matching task used by Hagelthorn et al. (this issue), although results from a patient with anterior section of the callosum (Copeland & Zaidel, 1997) indicate that such regions may be critical in both tasks. Finally, it appears that interhemispheric interactions can be asymmetric even within the same callosal pathways (Brown, Larson, & Jeeves, 1994). This asymmetry may be subject to a developmental process. These results suggest that although we talk about *interhemispheric interaction*, that term probably really reflects a family of means and mechanisms of interchange that may more appropriately be termed *interhemispheric interactions*.

LIFE-SPAN CHANGES IN INTERHEMISPHERIC INTERACTIONS

Other articles in this issue consider life-span topics from the perspective of both young children and aged adults. Using the dichotic listening task as a proxy for

interhemispheric interaction, Cowell and Hugdahl (this issue) examined the various aspects of individual differences that may influence this function. In particular, they examined effects of gender and handedness, which have been discussed for over a decade as having an effect on callosal morphology (e.g., Witelson & Goldsmith, 1991). Their results indicate that the effects of these variables are likely to be interactive, which suggests that uncovering the exact nature of the relations of these characteristics to callosal function in dichotic listening is likely to be somewhat daunting.

In addition to effects of gender and handedness on callosal functioning, there is also evidence of the effects of adult aging. The article by Reuter-Lorenz and Stanczak (this issue) shows that with age there is a greater benefit from interhemispheric interaction at lower levels of computational complexity. This finding suggests a greater need for division of information processing between the hemispheres with advancing age, which the authors link very nicely to functional neuroimaging studies of aging. One pattern found in neuroimaging studies of aged individuals is that the elderly are more likely to show bilateral activation, as compared with younger adults (e.g., Cabeza et al., 1997). Rather than positing a breakdown of localization of function, known as *dedifferentiation*, Reuter-Lorenz and Stanczak proposed on the basis of the interhemispheric work that this pattern of bilateral activation in the aged brain reflects an invoking of mechanism of interhemispheric interaction to deal with the reduced computational capacity of the single hemisphere.

INTERHEMISPHERIC INTERACTIONS AND COMPROMISED CALLOSAL INTEGRITY

Another theme of the articles within this issue is how we can be informed about interaction between the hemispheres by examining interchange in individuals who lack or have compromised callosal function. The article by Chicoine et al. (this issue) provides a striking display of how the performance of young children, aged 6 to 7 years, on a visuomotor task looks very similar to the performance of individuals who lack a callosum and have only an anterior commissure available for direct cortical-cortical transfer. The converging perspective provided by such evidence allows us to have much greater certainty that the deficit observed in young children on the same task is the consequence of immature callosal function, rather than limitations in intrahemispheric processing resources.

The article by Banich, Passarotti, White, Nortz, and Steiner (this issue) takes a different perspective in examining a population of children, those with early-treated phenylketonuria (ETPKU), who are likely to have atypical myelination, which would affect the corpus callosum. Unlike neurologically intact young children, who seem to rely on an even greater degree of interaction between the hemispheres to

compensate for computational complexity, children with ETPKU do not appear to have such an option available to them. Apparently, reduced callosal function due to the phenylketonuria reduces callosal interactions such that interhemispheric sharing of information is diminished. As a result, bihemispheric sharing of processing is not advantageous, and children with ETPKU do not exhibit the typical across-hemisphere advantage.

A SUMMARY OF THE DYNAMICS OF INTERHEMISPHERIC INTERACTIONS AND CALLOSAL FUNCTION

Given all these different perspectives that are provided by life-span studies, can we come to some general conclusions about callosal function? We believe that there are some common themes that are revealed across this series of articles. Expanding somewhat on the Banich and Belger (1990) model, we would theorize that there are three major factors that influence callosal interactions and that determine whether dividing processing across the hemispheres is helpful to task performance. These factors are (a) the degree to which the processing resources of a single hemisphere are taxed by the computational complexity of the task in a given individual, (b) the degree to which a communication overhead is imposed by callosal transfer, and (c) whether the informational complexity of the stimulus to be transferred exceeds the channel capacity of the callosum (or of the noncallosal commissures) of the individual.

The work presented within this issue provides support for such a conceptualization. The work of Banich and colleagues (Banich & Belger, 1990; Belger & Banich, 1992, 1998) has demonstrated that when tasks are computationally simple, it is actually advantageous to have information be processed by a single hemisphere. Because the processing resources of one hemisphere are ample for the task, only the communication overhead imposed by callosal transfer slows processing. On such tasks, bilateral disadvantages are seen, and the degree of disadvantage suggests the functional state of the callosum.

A similar issue is the complexity of the stimulus material itself, particularly with respect to the channel capacity of the corpus callosum, anterior commissure, and other pathways available. Here, the prediction is that individuals without a corpus callosum should not exhibit much of a transfer deficit for very simple stimuli, and this is indeed the case (Kreuter, Kinsbourne, & Trevarthen, 1972). In fact, there are some simple across-hemisphere matching tasks that can be done in the absence of the corpus callosum. What these studies reveal, however, is that the complexity of the information influences whether it can be transferred by noncallosal fibers. Work by Brown et al. (1999) reveals that ACC individuals with only an anterior commissure can transfer information about simple, overlearned,

and easily encoded stimuli (such as letters), especially when the set of possible items and responses is limited. However, as the information complexity of the stimuli to be transferred increases (e.g., complex visual patterns that cannot easily be labeled), the available anterior commissure cannot support transfer. Jeeves and Lamb (1988) made a similar argument regarding callosal channel capacity in a study in which the information necessary for interhemispheric stimulus comparisons could be measured in bits.

When task complexity increases to the point that the resources of a single hemisphere are overly taxed, another process comes into play. Under such conditions, it becomes advantageous to divide processing across the hemispheres so that more computational power can be brought to bear. Because both hemispheres can process almost all tasks to some degree (and perhaps in different manners), division of processing is possible. In such a case, it is assumed that the extra computational power brought to bear by interhemispheric division of processing more than offsets the overhead involved in callosal communication.

Let us examine the way in which such a model can explain the findings from the different clinical populations examined in this issue. In the elderly adults, we assume that each hemisphere has less computational power than that possessed by corresponding hemispheres of younger adults. Under such a conceptualization, the ability of a given hemisphere is more likely to be taxed at a lower level of complexity than in young adults, and there is a consequent need to switch to an across-hemisphere processing mode at a lower stage of computational complexity. Such a possibility is supported by recent data that demonstrated that the brain appears to be able to switch flexibly between a within- and an across-hemisphere mode of processing (or vice versa), depending on task demands (Weissman & Banich, 2000). Although there may be some loss of callosal connections in older adults (Janowsky, Kaye, & Carper, 1996), these probably do not yield an exaggerated effect of aging as compared to the effects of aging on the processing capacity of the cerebral cortex itself. Thus, because intrahemispheric resources are exceeded more readily in older adults, relatively more intact callosal function allows for greater advantages to accrue from splitting processing demands between the hemispheres. Hence, the greater bilateral advantage demonstrated at lower levels of task complexity in the aged probably reflects loss of intrahemispheric processing resources.

The inability of younger children to perform the visuomotor task used by Chicoine et al. (this issue) when tested with the unpracticed hand appears to be due not to limitations in intrahemispheric resources, but rather to the complexity of the information that must be transferred interhemispherically. The finding that individuals with ACC also fail to transfer the learning to the unpracticed hand suggests that the information that must be transferred is too complex for alternative interhemispheric pathways. Hence, the lack of across-hemisphere transfer in younger children in this task probably reflects limitations in the channel capacity of the corpus callosum. Brown and Paul (2000) made similar comparisons between child

development and callosal agenesis with respect to reduced interhand transfer of the complex tactile–spatial information of the Tactile Performance Test.

Finally, with regard to children with ETPKU, there is no evidence that they exhibit a deficit on within-hemisphere trials compared with their neurologically intact peers. This suggests that the computational complexity of each hemisphere is not being disproportionately taxed in ETPKU as compared with age-matched individuals. Rather, either the lack of callosal myelination increases the general overhead of callosal transfer (i.e., increases interhemispheric transfer time) or, as in younger children, the callosum has been adversely affected so that it cannot support transfer of more complex information (i.e., channel capacity has been exceeded).

SOME REMAINING RESEARCH QUESTIONS

Although such a framework may help to explain some aspects of callosal function, there is another class of questions, not addressed by articles in this issue, that will need to be addressed in future work for us to adequately understand the nature of interhemispheric interaction. In the articles included in this issue, most of the authors have centered their investigations on how the corpus callosum affects the information-processing capacity of the brain across the life span. They do not address the question of the nature of the representation of information that is transferred across the hemispheres. For example, they do not answer the question of how facial features analyzed by the left hemisphere are integrated with information about the gestalt of a face processed by the right hemisphere. How do these two types of information get integrated? Stated metaphorically, if the left hemisphere is thinking in French and the right in English, what language do they use to communicate—French? English? or some other language? Does the “language” of interhemispheric interactions and callosal transfer change with age, with changes in callosal integrity, or with different task demands? We hope that this issue serves to provoke a larger discussion about how information processing is integrated across the hemispheres (and between other brain regions) over the process of life-span development.

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